

THE TAXONOMIC STATUS OF *TILIA DASYSTYLA* IN CRIMEA, UKRAINE

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Nine populations of *Tilia dasystyla* Steven (*Tiliaceae*) in the Crimean mountains (Krymskiye Gory), including the type locality at Kastel Dag, were studied in the field and sampled by collection of herbarium specimens. This material was compared with specimens referred to *Tilia begonifolia* Steven collected in Crimea, the Caucasus and Iran. Measurements or scores of 21 morphological characters made on the dried material were analysed by principal components analysis and logistic regression. These analyses demonstrated that the majority of trees could be correctly allocated to either Crimea or the Caucasus and Iran on the basis of the shape of their leaves and the area of their bracts. In addition there are differences of leaf and bract texture and bract colour which can be observed in fresh material. Chromosome counts showed that Crimean trees and one Caucasian tree are tetraploid ($2n=164$). It is proposed that the Crimean, Caucasian and Iranian trees be treated as a single species with at least two subspecies: *Tilia dasystyla* Steven subsp. *dasystyla* from Crimea and *T. dasystyla* Steven subsp. *caucasica* (V. Engl.) Pigott from the Caucasus and Iran.

Keywords. Caucasus, chromosome numbers, Crimea, logistic regression, new combination, *Tilia*.

INTRODUCTION

Three species of *Tilia* were regarded by Maleev (1949) as native in Crimea, all restricted to the hills (Krymskiye Gory) in the south-western part of the peninsula (Fig. 1). *Tilia cordata* Mill. is here at its southern limit and, as in the Caucasus and Mediterranean region, most populations grow on north-facing slopes or in ravines (Pigott & Pigott, 1993). Specimens in the herbarium of the Nikita Botanic Garden at Yalta (YALT) are typical for the species throughout most of its range and present no taxonomic problems. The other two taxa, treated by Maleev as species, are the subject of this paper.

Tilia caucasica Rupr. was reported by Maleev as occurring throughout mountainous Crimea. This taxon is widespread in the Great and Little Caucasus, where it usually occurs with beech (*Fagus orientalis* Lipsky) in the altitudinal range of 500–2000m above sea-level (Tsepilyaev, 1965). It also occurs in the mountains of northern Turkey (Yaltirik, 1967). Maleev treats the taxon in the eastern part of the Little Caucasus (including Nagorno Karabakh) and in the Elburz mountains of Iran as a separate species, *T. begonifolia* Steven, but Browicz (1981) regards this as a synonym of *T. caucasica*, which, however, the former predates (see Appendix).

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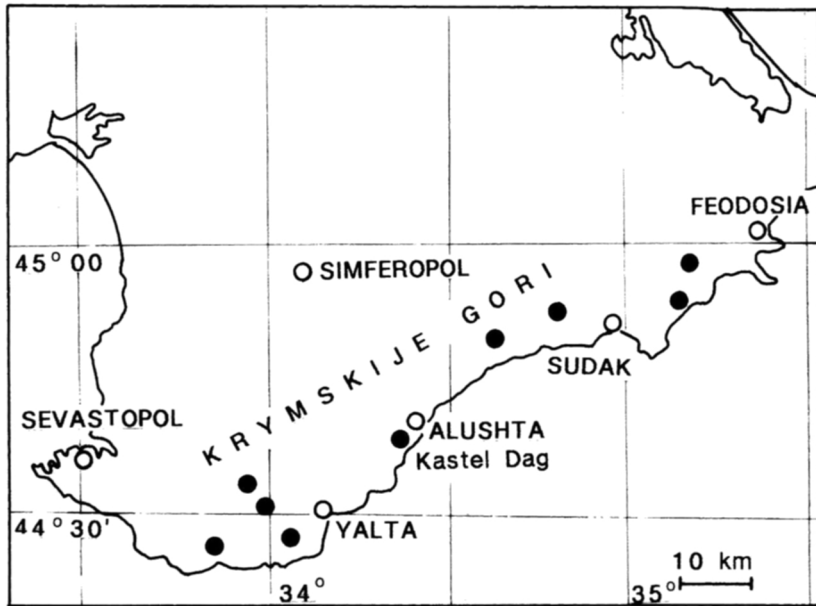


FIG. 1. Map of the southern part of Crimea showing the distribution of populations of *Tilia dasystyla* subsp. *dasystyla* studied (●) and the principal towns (○). Based on Turistskaiya Karta 1:100 000 Krim.

The third taxon, *T. dasystyla*, was described by Steven (1832) from Kastel Dag near Alushta in Crimea. Maleev (1949) states that it is probably endemic to Crimea and is reliably recorded from eight to 10 localities which are mainly on the southern slopes of the hills. He emphasized the need for further study.

Although there are many specimens of *Tilia* from the Crimea in Russian and Ukrainian herbaria, there has been no systematic sampling to establish the extent of variation within populations. Also, many specimens identified as *T. caucasica* are non-flowering shoots. To remedy these limitations a visit by one author (CDP) to Crimea in July and August 1992, accompanied by Sheila Pigott and by Vladimir Schatko and Inessa Volkovskaya of the Botanical Society of the Russian Republic, allowed nine separate populations of *Tilia* to be studied, including that at the *locus classicus* of *T. dasystyla* at Kastel Dag (Steven, 1832). Herbarium material was collected from 52 individual trees and seedlings from four populations were subsequently grown in the University Botanic Garden in Cambridge. Most of the material from the Caucasus, which was used for comparison, had been collected on two earlier visits to the Georgian Republic in 1988 and 1990.

MATERIAL AND METHODS

Sampling

Nine populations of *Tilia* were sampled at widely separated sites along the Krymskije Gory, over a distance of about 100km, from the high cliffs and screes (820–860m

alt.) above Alupka (44°26'N 34°02'E) in the west to the largely wooded hills of Legener Gora and Echki Dag near Shchebetovka (44°57'N 35°09'E) in the east (Fig. 1). Eight of these sites are on hard Mesozoic limestone: the ninth is on a massive block scree of quartz diorite and quartz porphyry at the eastern foot (120m alt.) of Kastel Dag near Alushta (44°41'N 34°24'E). Of these nine populations six had been previously recorded as *T. dasystyla*, two as *T. caucasica* (= *T. begonifolia*) and one as uncertain.

At each site the aim was to obtain unshaded shoots with flowers or fruits from the main canopy of up to 10 trees. In most cases these shoots could be reached relatively easily, sometimes by climbing, because many of the trees grow on cliffs, block scree or very shallow soils over rock and are only 4–10m tall. The material was examined fresh and then herbarium specimens were made of shoots with about 20 leaves and 10 inflorescences. This material is preserved in the personal herbarium of C.D. and S. Pigott. For each tree a record was made of the slope, aspect, type of habitat and closely associated woody species. Altitudes were obtained from maps (Turistskaiya Karta 1:100 000 Krim).

The specimens from the Caucasus used for comparison were also collected from the main canopy of trees in natural populations but usually at the edge of woodlands. This was because most trees were in high forest of *Fagus orientalis* and their main canopy was over 10m from the ground and inaccessible with the facilities available. Five widely separated sites were sampled. Three sites were in the Great Caucasus at Lagodekhi (41°50'N 46°16'E) near the border of Azerbaydzan, above Mtisdziri near Kvareli (41°57'N 45°48'E) and near Gombari (41°52'N 45°14'E). Two were in woodlands in the Little Caucasus near Tetriskalo at 41°36'N 44°28'E and at 41°22'N 44°20'E further to the south-west. Additional specimens from trees in villages were used for comparison but not for analysis. Three specimens from Iran were supplied from the Botanical Institute in Tehran. This material was supplemented with specimens from herbaria (LE, BM, K, E) where these had the required numbers of undamaged leaves and bracts.

Measurements

Thirty measurements and two scores on arbitrary scales were made on each of 79 specimen of the characters listed in Table 1. Other characters were recorded or measured on the fresh material or dried specimens. For example, some trees, particularly at higher altitudes, were still in flower, while the majority were in various stages of development of the fruit but these usually retained styles on the younger fruits on which the distribution of hairs could be recorded.

Statistical analysis

A preliminary analysis was made using principal components analysis (Krzanowski, 1988: 254). Subsequent analysis was designed to discriminate between the material

TABLE 1. Measurements and scores which form the basis of the statistical analyses (all measurements in mm)

1	Length and breadth of three largest leaves, to give values for a single leaf, selected as the mode of the product of length and breadth
2	Mode of length of three petioles
3	Base of leaf lamina scored as: (1) deeply cordate, (2) shallowly cordate, (3) cordate on one side of midrib and truncate on other, (4) truncate and (5) obliquely truncate
4	Mode of length of acumen of lamina of three leaves
5	Mode of number of pairs of lateral veins on three laminae
6	Hairs on lamina scored as: (1) none, (2) groups of fasciculate hairs in vein axils on abaxial surface, (3) as 2 and with hairs along main veins, (4) as 3 and with hairs on minor veins and (5) as 4 and with hairs on adaxial surface
7	Mean of number of teeth/10mm on three random lengths of lamina margin
8	Mode of length of three tips of marginal teeth
9	Length and breadth of three bracts to give values for a single leaf, selected as the mode of the product of length and breadth (referred to as bract area)
10	Mode of lengths of three peduncles (stalks of cymes)
11	Mode of lengths of three pedicels (stalks of flowers)

from the two geographical areas using logistic regression analysis (Krzanowski, 1988: 358; Collett, 1991); this method is preferable to linear discriminant analysis when the distributions are non-normal or the dispersion matrices are unequal. The software package used was GLIM release 4 (Francis *et al.*, 1993).

Chromosome counts

All counts were made on squashes of root-tips from young plants (1–4 years old), grown from fruits or seedlings in a 4:1 mixture of John Innes compost No. 1 and quartz sand. Root-tips were pretreated in 0.01% colchicine in water, fixed in a freshly prepared mixture of absolute ethanol (10 parts), chloroform (2 parts), glacial acetic acid (2 parts) and formalin (1 part) and stained in Feulgen's reagent. Counts were based on completed drawings made with a Nikon Optiphot/Labophot Drawing Device ($\times 1.25$) on a Nikon Optiphot binocular microscope with E Plan $\times 100$ oil immersion objective to give a total magnification of $\times 1250$. All plants counted have been retained and some are now planted in the University Botanic Garden at Cambridge. Specimens of the parent trees are preserved in the personal herbarium of C.D. and S. Pigott but the actual plants counted are still immature and unsuitable as vouchers.

RESULTS

General morphology

In comparison with other European species of *Tilia*, all the trees studied in Crimea are remarkable for the general uniformity of their appearance. Fresh unshaded

flowering or fruiting shoots of all the trees possess the same striking features of texture and colour which are largely lost in dried material. The small circular and rather thick leaves have their upper surface dark green and lustrous and the lower surface pale green but not glaucous. The narrow elliptical bracts are stiffly recurved at the junction with the peduncle, yellowish green and have a shining waxy surface. These features of the bract are seen and are more familiar in the widely planted *T. × euchlora* C. Koch: this is almost certainly a hybrid between *T. dasystyla* and *T. cordata* which is sterile and probably triploid. The shaded shoots and juvenile shoots of the Crimean trees, in contrast, show none of these features.

These same characters differentiate the Crimean trees from most of the trees of *T. begonifolia* studied in natural populations in the Great and Little Caucasus. In general, the leaves of Caucasian trees are larger and more coarsely toothed, they lack the lustre on their upper surface, and the bracts are much larger, elliptical or oblanceolate, not stiffly recurved but more or less flat, or undulate in the lower part, and pale green.

Those characters which can be measured or scored on all the dried material form the basis of the following analysis. Characters of the flower and fruit are omitted because the specimens are at different stages of development, as is also generally the case in herbarium specimens.

Data from 79 specimens were analysed consisting of 51 specimens from Crimea, 27 from the Caucasus and Iran and one from Turkey (E13755), included because it closely resembled the Crimean specimens. Median values of length and breadth of leaves and of length and breadth of bracts were calculated for each tree from sets of three measurements from each specimen. All variables measured are continuous apart from the classifications of the shape of the leaf base and the distribution of hairs. Both of these are ordinal and each can be treated as a continuous score representing respectively, the transition from cordate to obliquely truncate leaf bases, and the degree of hairiness of the leaves. Six specimens (five from the Caucasus and one from Crimea) had incomplete data on at least one variable, leaving 73 specimens for the primary statistical analysis. These were reinstated in the final analyses because only significant variables were included for which they were complete.

An exploratory investigation of the data using principal components analysis ignored the geographical source of the specimens and yielded four principal components with eigen values above 1, together explaining 69% of the variation of the data. The first principal component explained 39% of the variation, and loaded high and positively on the four bract and leaf dimension variables; the second component explained an extra 11% of the variation, with pedicel length having a high positive loading and leaf base score a high negative loading. Figure 2 displays the first two principal component scores, identifying the provenance of each tree. In the first dimension the Caucasian trees tend to have larger leaves and bracts than the Crimean trees: from the second dimension there is evidence that the Crimean trees have longer pedicels and their leaf bases are more likely to be cordate than truncate. The Turkish specimen falls within the Crimean group. It is clear that principal component analysis

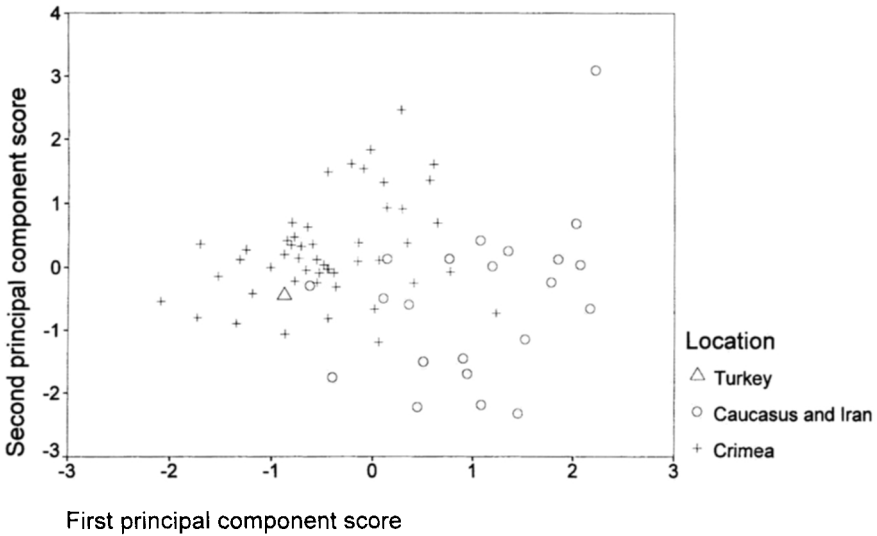


FIG. 2. Results of the principal components analysis, plotting the second against the first component score for each specimen of *Tilia dasystyla*.

separates the two provenances to some extent but there is still overlap. We therefore proceeded to a logistic regression and attempted to find the best combination of variables which will discriminate between the groups.

The logistic regression, which modelled the probability of a specimen being of Crimean provenance (omitting the single Turkish specimen) proceeded in two stages. As principal components analysis identified leaf and bract lengths and breadths as being particularly important, these variables were examined in detail in a separate logistic regression. The results showed that the estimates for bract length and breadth had estimates nearly equal in size and sign, suggesting that an overall measure of bract size such as bract area would be most effective in subsequent analysis. Parameter estimates for leaf length and breadth, however, gave estimates which were nearly equal in size but of opposite sign, suggesting that a measure of leaf shape (that is, long and narrow versus short and wide) would be most appropriate.

Two new variables were therefore constructed, consisting of median bract area (defined for this purpose simply as the product of length and breadth, which is on average the true area $\times 1.55$, and used from this point on with this meaning) and median leaf shape (defined by the difference of length minus breadth). A logistic regression including these variables as covariates with the earlier set and using a forward selection procedure based on the log-likelihood test statistic was then carried out. The results are summarized in Table 2. Only two variables were significant: leaf shape and bract area. All but three of the 72 trees were classified correctly. Table 3 gives the parameter estimates from the logistic regression. These can be used to define a score:

TABLE 2. Results of logistic regression of specimens of *Tilia*, modelling the probability of the specimen originating from Crimea

Model	-2 log likelihood	Degrees of freedom	Change in -2 log likelihood	Change in df	P value
Constant probability	88.63	71			
Bract area	25.98	70	62.65	1	<0.0001
Bract area + leaf shape	22.83	69	3.85	1	0.05

TABLE 3. Estimates of parameters from logistic regression

Parameter	Estimate	Standard error
Constant	7.791	1.970
Bract area	-0.0057	0.0017
Leaf shape	-0.118	0.065

$$\text{SCORE} = 7.791 - 0.0057 * \text{bract area} - 0.118 * \text{leaf shape}$$

or, scaling the score so that the coefficient for bract area is unity and rounding the other coefficients to the nearest whole number, a close approximation is obtained:

$$\text{SCORE} = 1367 - \text{bract area} - 21 * \text{leaf shape}$$

which can be used to classify new specimens. If the score is greater than zero, then the estimated probability of the specimen originating from Crimea is greater than 0.5, and the estimated group membership is taken to be Crimean. If the score is less than zero, the predicted group is Caucasian. Figure 3 shows a plot of leaf size against bract area, identifying the location of each tree and superimposing a solid line with score equal to zero. Trees which fall below the line are predicted to be Crimean; those falling above the line are predicted to be Caucasian and Iranian.

All 79 trees can, in fact, be classified, as there are no missing values for bract and leaf length and breadth. Predicted scores for the Crimean trees range from 150 to 1394, except for one tree with a negative score (-650). Predicted scores for the Caucasian and Iranian trees range from -119 to -2752, except for four trees with small positive values (10.5, 30, 279 and 316). The Turkish tree (which was included because it appeared to be like the Crimean) has a score of 379, which implies that the tree is more like the Crimean than the Caucasian type.

Chromosome number

Chromosome numbers for six plants from four Crimean populations and one plant from the Great Caucasus are given in Table 4. The chromosomes of *Tilia* are small

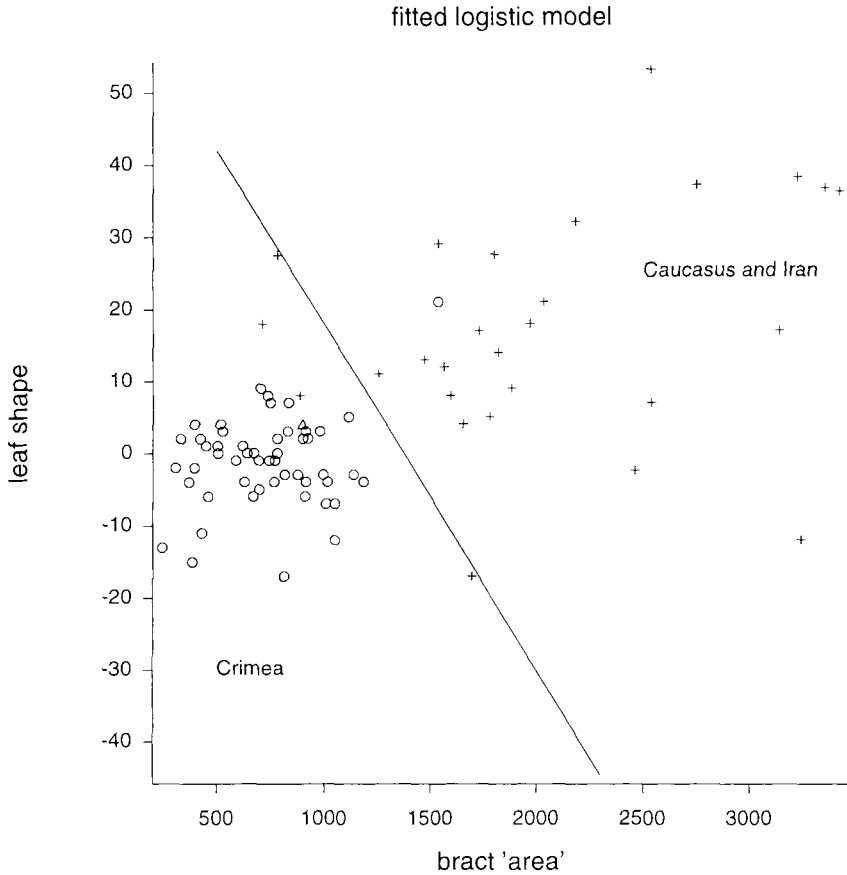


FIG. 3. The fitted logistic model, plotting values of leaf difference against those of bract area for each specimen of *Tilia dasystyla*. Points below the line are predicted to be trees of Crimean provenance; points above the line trees of Caucasian and Iranian provenance. Symbols have the same meaning as in Fig. 2.

(c.1.0 μ m long) so that it is often difficult to obtain exact numbers. Nevertheless, the somatic number of $2n = 164$ was established with reasonable certainty for three plants (reference numbers 234, 247 and 284) and, although the maximum numbers that were counted for two plants (127 and 302) did not exceed $2n = 160$, sufficient uncertainty existed in the best preparations that the higher number of $2n = 164$ was still possible. For two of the plants (067 and 225), on the other hand, the highest numbers counted on strongly stained and well-spread squashes with no evidence that the metaphase plates had been disrupted, were respectively $2n = 150$ and $2n = 156$. Overall, the counts demonstrate that the Crimean plants and the one from the Caucasus are tetraploids and therefore differ from the other European species where all plants so far counted have been diploids ($2n = 82$).

TABLE 4. Somatic chromosome numbers of Crimean and Caucasian plants of *Tilia dasystyla* subsp. *dasystyla* (067–284) and subsp. *caucasica* (302)

Reference	Locality	Numbers counted	Highest number counted
067	Legener Gora near Shchebetovka	144–150	150
127	Mountain between Voron and Medjdureche, Crimea	158–160	160
225	Chertova Lestnitsa above Alupka, Crimea	154 156	156
234	Echki Dag near Shchebetovka, Crimea		164
247	Chertova Lestnitsa above Alupka, Crimea		164
284	Echki Dag near Shchebetovka, Crimea		164
302	Lagodekhi, Great Caucasus	154–159	159

DISCUSSION

Tilia dasystyla was described by Steven (1832) from a single tree at Kastel Dag near Alushta. The holotype is at Helsinki (H, 1107996) and there are isotypes at St Petersburg (L), Kew (K) and probably elsewhere. Steven based his separation on the hairiness of the style, which in the type material is densely covered with fasciculate hairs along its entire length. In the original description Steven states '*ad radices montis Casteldagh juxta viam publicam unicam arborem vidi*' ('at the foot of mount Casteldagh beside the public road a single tree was seen'). In 1992, however, at least 17 old trees (some judged by their girth were certainly older than 160 years) were still present on block scree beside the old road, and other trees might have been lost since 1832 because of a quarry between the new and old roads. Eleven of these trees were successfully sampled and were included in the statistical analyses which show that they fall well within the range of variation of the trees of Crimean provenance. There is variation between individual trees in the shape of the fruits (from broadly ellipsoidal to obovoid) and in the height to which a dense cover of hairs extends from the base to the top of the styles. It seems improbable that Steven saw only one tree at this site, so his statement probably means that only one tree had a completely hairy style.

The same variation in hairiness of the styles was noted in all the Crimean populations studied in 1992. Loria (1967), who studied more than 3500 specimens, described similar variation throughout the entire Caucasian region and dismissed the taxonomic value of the character, Largely on this basis, Loria regarded the Crimean, Caucasian and Iranian populations of *Tilia* as belonging to a single taxon

which he treated as a distinct subspecies of the European species *Tilia platyphyllos* Scop. In addition to the differences in the leaves used by Loria (1967) to separate his Caucasian, Iranian and Crimean subspecies, it has smaller fruits which have thinner and weaker walls. These characters, in fact, provide more reliable morphological distinctions. The present study also demonstrates that the Crimean and probably the Caucasian taxa are tetraploid ($2n=164$) while European *T. platyphyllos* is diploid ($2n=82$). This gives added weight to keeping the Caucasian and Crimean plants on the one hand and European *T. platyphyllos* on the other, as separate species.

Loria's extensive study of Caucasian and Crimean material makes no mention of the size and form of the bracts, nor the size, shape and texture of the leaves on the flowering shoots. The inclusion of specimens of non-flowering shoots might have obscured the difference between trees of these two provenances because the leaves of basal shoots and the lower part of the canopy of Crimean trees are large and thin, and appear very like those of Caucasian trees. For example, many, if not all, of the specimens in the herbarium at Nikita (YALT), which were collected in Crimea and have been referred in the past to *T. caucasica* Rupr. (*T. begonifolia* Steven), are sterile shoots either from basal sprouts or from the lower part of the canopy of trees in woodland; often these are the only easily reached specimens. When shoots were obtained from the emergent crowns of tall trees regarded as *T. begonifolia* that were growing in dense woodland on the northern slopes of the hills above Yalta on the road to Bachschisarai, they proved to be typical of the Crimean race, and this is confirmed in the present analysis.

The morphological analysis presented here is based on 51 trees from nine populations in Crimea and a very limited but non-selective sample of trees from the Caucasus and Iran. The results of the principal components analysis of all the variables measured show that trees of Crimean provenance tend to differ from those of Caucasian provenance in the shape and size of their leaves and bracts, in pedicel length and in the form of the leaf base, but there is considerable overlap. Logistic regression shows that the area of the bracts, as an overall measure of their size, and the shape of the leaves, expressed by the relation between length and breadth, allows almost all of the 72 trees to be correctly allocated to their provenance. This analysis demonstrates the reality of the general observations that Crimean trees have small, narrowly elliptical bracts and almost round cordate leaves, whereas Caucasian and Iranian trees have larger, usually oblanceolate bracts and longer, often obliquely truncate leaves. To this separation might be added the differences in colour and texture of the bracts, which in Crimean trees are pale yellowish green, waxy textured and characteristically reflexed at the junction with the peduncle, and in Caucasian trees are pale green, dull and often slightly undulate at the margin near the base and never stiffly reflexed. As well as the difference in shape of the leaves, there is the thicker lamina and lustrous upper surface of the leaves of the Crimean trees, in contrast to the thinner lamina and dull upper surface of the Caucasian trees.

The fundamentally quantitative nature of the differences and the evidence that both provenances are tetraploid are the basis of the proposal that they should be

treated as geographically separated subspecies of one species. It is probable that with further investigation of Caucasian, Turkish and possibly Greek populations of *T. dasystyla* other subspecies will be recognized. A summary of the diagnostic characters follows:

Tilia dasystyla Steven in Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 4: 260 (1832). Type: 'Casteldagh; Taur. merido. juxta viam inter Alustem et ...' [Crimea, Kastel Dag near Alushta], *C. Steven* (holo. H-1107996; iso. K, LE).

Tilia dasystyla Steven subsp. ***dasystyla***

Lamina of leaves 48–82 × 47–81 mm, circular, the base usually cordate, rarely truncate, marginal teeth small 4.9/10 mm, triangular, acute with a tip 0.6–1.7 mm long; upper surface dark green, glossy when fresh; lower surface pale green (not glaucous), dull, with groups of light brown fasciculate hairs in the axils of the main veins. Bracts 48–77 × 8–16 mm, stiffly recurved at the junction of the peduncle, narrowly elliptical, subacute at the apex, pale yellowish green, shining, waxy. Flowers 12–15 mm diam., styles glabrous or hairy for part or the whole of their length.

Tilia dasystyla Steven subsp. ***caucasica*** (V. Engl.) Pigott, **comb. nov.**

Basionym: *Tilia rubra* DC. subsp. *caucasica* V. Engl., Monogr. Tilia, 617 (1909). Type: as for *T. begonifolia* Steven.

Syn: *Tilia platyphyllos* Scop. subsp. *caucasica* (V. Engl.) Loria in Bot. Zurn. SSSR 52: 1790 (1967).

Tilia begonifolia Steven in Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 29: 326 (1856). Type: [Armenia] In sylvis Karabagh orient. 829, Herb. Steven, (holo. H-1107877!, iso. LE!).

Tilia caucasica Rupr. in Mém. Acad. Imp. Sci., Saint Petersburg: Seconde Pt. Sci. Nat. 15: 253 (1867), *nom. illegit.* (Art. 52.1).

Lamina of leaves 66–126 × 52–106 mm, circular to ovate, the base shallowly cordate or obliquely truncate, apex acuminate, marginal teeth 3.8/10 mm, triangular acute, the tip 0.7–1.7 mm long; upper surface green, more or less dull, lower surface paler green, dull, with groups of light brown fasciculate hairs in the axils of the main veins. Bracts large, 76–141 × 11–26 mm, oblanceolate, often undulate at the margins near the base, rounded at the apex, not stiffly recurved at the junction with the peduncle, pale green, dull. Flowers 12–16 mm diam., styles glabrous or sometimes as in the type subspecies.

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APPENDIX

Nomenclature of the Caucasian taxa of Tilia

The earliest validly published name to have been frequently used for the Caucasian taxon is *T. rubra* DC. (1813: 215), to which De Candolle also gave the name '*Tilleul à bois rouge*'. There are two specimens at Geneva labelled by De Candolle '*Tilleul à tiges rouge*' which must be regarded as syntypes. The smaller, undamaged specimen with three leaves and two bracts, which is mounted on the same sheet as a separate specimen labelled *T. platyphylla*, is here designated the lectotype of *T. rubra* DC. Rehder (1923, and in a letter preserved at Geneva) correctly identified these as the variety of *T. platyphyllos* with red twigs and the original

description states '*folia subtus pilosiuscula ut in T. platyphylla*' which would apply to *T. platyphyllos* but not to the Caucasian taxon (i.e. *T. dasystyla* subsp. *caucasica* see below). The name *T. rubra* DC. is therefore a synonym of *T. platyphyllos*.

There are also two specimens labelled *T. rubra* by De Candolle, which were sent to him by Steven in 1817 and in 1818, both from Tauria (Crimea) but these postdate the publication of the name and cannot be regarded as types.

The next validly published name within the group is *T. dasystyla* Steven (1832: 260) for a Crimean plant. As the Crimean, Caucasian and Iranian plants are here treated as a single species, this name has priority. The earliest name for the Caucasian taxon, when treated as a subspecies, is *T. rubra* DC. subsp. *caucasica* V. Engl. (Engler, 1909: 617), so that this name is used here to form the new combination *T. dasystyla* subsp. *caucasica* (V. Engl.) Pigott. This retains this epithet for the taxon for which it has been widely used.

If, however, the Caucasian and Iranian plants are treated as a separate species, the earliest name at species rank is *T. begonifolia* Steven (1856: 326), based on a specimen (now in Helsinki (H), iso. LE) sent to Steven by Szovitz from Karabagh in Armenia. This is Nagorno Karabagh at the eastern limit of the the Little Caucasus. The opening sentence of Ruprecht's description of *T. caucasica* (1869: 253) states that it includes all the species recorded from the Caucasian provinces. This implies that some of these species were erroneously recorded but, by including *T. begonifolia* Steven from Karabagh, Ruprecht rendered his new name illegitimate.